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Escape from competition: Neighbors reduce *Centaurea stoebe* performance at home but not away

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Abstract. The greater abundance of some exotic plants in their nonnative ranges might be explained in part by biogeographic differences in the strength of competition, but these competitive effects have not been experimentally examined in the field. We compared the effects of neighbors on the growth and reproduction of spotted knapweed (*Centaurea stoebe*) in Europe, where it is native, and in Montana, where it is invasive. There were strong negative competitive effects of neighboring vegetation on *C. stoebe* growth and reproduction in Europe. In contrast, identical experiments in Montana resulted in insignificant impacts on *C. stoebe*. Although the mechanisms that produce this dramatic biogeographic difference in competitive outcome remain unknown, our results indicate that differences in net competitive interactions between ranges may contribute to the striking dominance of *C. stoebe* in parts of North America.

Key words: biogeography; *Centaurea stoebe*; competition; exotic invasion; invasion success; spotted knapweed.

INTRODUCTION

Competition has long been thought to have strong effects on the distribution and abundance of plant species (Gurevitch 1986, Grace and Tilman 1990, Pennings and Callaway 1992). If negative competitive interactions constrain the abundance and performance of species in native communities, then any weakening of these competitive effects against introduced exotics might help explain why some exotics can attain high densities in their nonnative ranges (e.g., Ortega and Pearson 2005, Hejda et al. 2009). Biogeographical differences in relative competitive intensities may also help to explain invader impacts, i.e., the ability of some invaders to competitively suppress natives in the new ranges of the invaders (Vilà and Weiner 2004, He et al. 2009, Maron and Marler 2008a, Inderjit et al. 2011).

Why might the effects of neighboring plants be generally less harmful to an exotic in recipient communities than at home? Several hypotheses have been put forth to explain this. One possibility is that release from host-specific enemies may drive biogeographic differences in the ability of an exotic to compete with surrounding plants at home and abroad (Elton 1958, Keane and Crawley 2002, Kulmatiski et al. 2008). In this scenario, specialist herbivores and/or pathogens sup-

press exotics where they are native, but liberation from these enemies enables exotics to outcompete natives in recipient communities, and particularly if natives have to cope with their own enemies. One problem with this hypothesis is that it predicts that factorial experiments that manipulate competition and herbivory should demonstrate strong competition by herbivory interaction for native plants. Yet, while there are certainly cases in which competition and herbivory interact synergistically to suppress plant performance, there is little evidence for clear competition by herbivory interactions for exotic invasive plants. Another possibility is that some invaders have unique life-history attributes compared to plants in a recipient community. These traits might enable an exotic to access resources that natives cannot (Mack et al. 2000), alter native ecosystems in ways that benefit the invaders (D'Antonio et al. 2001), or provide advantages through novel chemistry (Callaway and Ridenour 2004, Kim and Lee 2010).

Regardless of the mechanism, the general question of whether invaders show fundamentally different competitive interactions with the natives in their home range vs. natives in their invaded range has not been addressed in the field. What has been examined is how strongly native plants resist invasion by exotics. For example, in field plots where experimental invasions were staged within monocultures of natives, Maron and Marler (2008a) found that the biomass of *Centaurea stoebe* was unaffected by competition imposed by any of 10 different species of natives. Two other exotics, *Potentilla*

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recta and *Linaria dalmatica*, were only weakly resisted by competition from native plant species. Greenhouse experiments have also compared the competitive effects of invaders on species from their native and introduced ranges. These experiments have indicated that an invader can have more potent negative impacts on evolutionarily naïve neighbors compared to those from its native range (Callaway and Aschehoug 2000, Kim and Lee 2010, Ni et al. 2010). Finally, the extent to which exotics suppress natives varies with competitive conditions, such as the diversity of the invaded community (Maron and Marler 2008b).

Despite the importance of understanding how competition may change as a plant moves from its native to its introduced range, we know of no study of this biogeographical comparison. Here we report on such a study of *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek (spotted knapweed; see *C. maculosa* Lam.; see Plate 1), a native of Europe, but an invader in North America. We compared the response of *C. stoebe* to experimental neighbor removal between grassland sites in Europe and in Montana, USA.

METHODS

For the experiment, we selected five sites in Europe, where *C. stoebe* is native and occurs at relatively high densities for the native range (based on qualitative observations; cf. Treier et al. 2009), and nine sites in Montana, where *C. stoebe* occurred at relatively low densities for its invaded range (Appendix). Although *C. stoebe* can form near-monocultures under some conditions in its nonnative range, we avoided these sites so as to have a more even comparison to sites in the native range. The native range of *C. stoebe* is much larger than the scope of our experimental sites, with a few populations extending into France to the west and east to Russia and westernmost Asia. However, based on current molecular evidence, it appears that North American populations originated from Eastern Europe (Marrs et al. 2008) where we located our study sites. At all sites, the background plant community was grassland, with native grasses being the dominant functional type. In Europe, our choices ensured that *C. stoebe* was present at densities high enough to actually find enough young target individuals, whereas in Montana our choices ensured that target *C. stoebe* plants were surrounded by native species and not other *C. stoebe*. The five European sites were located in Romania and Hungary and the nine North American sites were all located in intermountain grassland in Montana. In Europe, the Máriakéménd, Perieni, and David's Valley sites were used in 2009 and the Pécsvárad and Barcs site were used in 2010. In Montana, the Perma, Grant Creek, Weed Office, and Nine-Mile Prairie sites were sampled in 2009 and the Schwartz Creek, Cyr, Marshall Canyon, O'Brien Creek, and Petty Creek sites were sampled in 2010. The experiment was also conducted at the Nine-Mile Prairie site in 2010, and we combined the

2009 and 2010 replicates and considered this as a single site. *Centaurea stoebe* exists in diploid and tetraploid populations in its native range, but exclusively in tetraploid populations in its nonnative range (Treier et al. 2009). All populations but one, David's Valley, were composed of tetraploid plants (see Appendix). The population at David's Valley, Romania, is diploid, but the mean competitive suppression of *C. stoebe* by neighbors was similar to that at the other site, suggesting that the inclusion of this site in our analyses was reasonable.

At each site we located 20 pairs of similar-sized *C. stoebe* plants in the late spring and randomly chose one of each pair for the control and the other for the experimental removal. For the removal of neighbors we placed a ring, 40 cm diameter, around the target plant and clipped all aboveground biomass inside of the ring, leaving just the target *C. stoebe*. We tried to choose small *C. stoebe* plants that had either just two mature leaves or were still small rosettes. This was easily accomplished in Montana where recruitment was extensive; however, this was more difficult in Europe simply because *C. stoebe* is less abundant, as are young recruits. Thus, at two sites, we had to use somewhat larger rosettes than were used in North America (Perieni and David's Valley), and at the Barcs site in Hungary we used plants that had just bolted because we could not find sufficient numbers of small plants. To determine whether the use of some larger target plants in Europe affected our results, we measured the number of leaves and the length of the longest leaf for each control and target plant and correlated mean initial size of plants at a site with the mean competitive response for European sites and North American sites. At the end of a single growing season, we counted all flower buds, flower heads, and seed heads on each plant, and then harvested the aboveground biomass of each plant, which was subsequently dried at 60°C and weighed. We used a mixed-model ANOVA (in SAS version 9.1 proc mixed module; SAS Institute 2002) to test the effects of region, site (nested within region), and treatment on *C. stoebe* aboveground biomass and reproduction (total number of flowers, buds, and seed capsules per individual). Site was considered a random factor and treatment and region were treated as fixed factors. Both response variables were log + 1-transformed. To examine how specific sites differed, we also conducted independent samples *t* tests for biomass and reproductive structures between the control and removal treatment for each site, and used *t* tests for the mean proportional effects of removing neighbors on biomass and reproductive structures in Europe vs. Montana.

RESULTS

At European sites the mean *C. stoebe* biomass increased 62–156% when neighbors were removed. In contrast, at Montana sites the effects of removing neighbors ranged from a decrease in mean *C. stoebe*

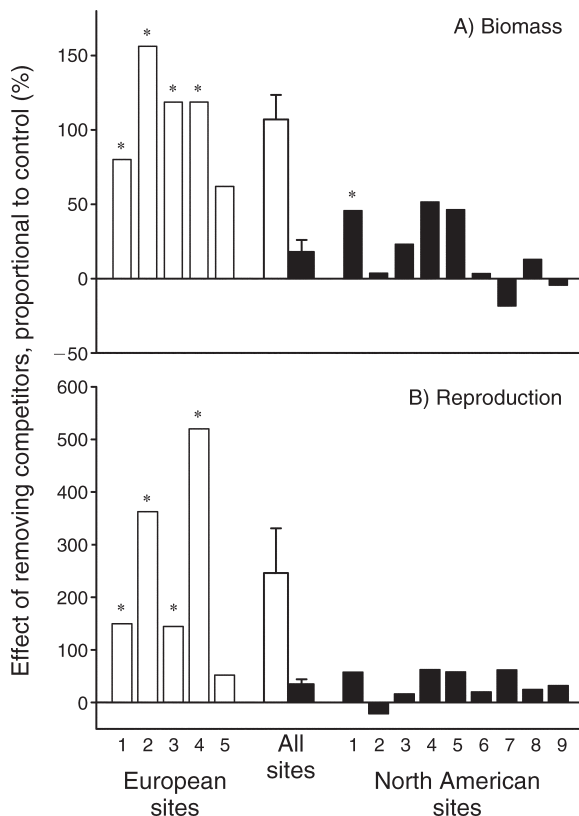


FIG. 1. Proportional (A) aboveground biomass and (B) reproduction of target *Centaurea stoebe* (spotted knapweed) plants in response to removing neighbors in the native range of Europe (open bars) and the nonnative range of North America (solid bars). Data are the (A) biomass or (B) number of flowering plants in removal treatments as a percentage of that in controls where neighbors were not removed. Bars without error bars are the mean response for each site, presented in the order shown in the Appendix. Bars in the middle of the graphs are the means for all sites within a region with the error bars representing \pm SE. Asterisks show significant differences ($P < 0.05$) between treatments and controls used to calculate the proportions at a single site as determined with separate t tests.

biomass of 18% to an increase of 52% (Fig. 1A). In Europe, the effect of competitors was significant at four of five sites and across all sites combined (neighbor removal, $F = 1.56$; $df = 1, 154$; $P < 0.001$). In Montana, the effect of removing neighbors was significant at only one of the nine sites and not significant across all sites combined (neighbor removal, $F = 20.14$; $df = 1, 362$; $P = 0.021$). The mean increase at the European sites was $107\% \pm 17\%$; whereas the mean increase at the Montana sites was $18\% \pm 8\%$; an approximately 6.5-fold difference in responses between regions (region, $F = 28.68$; $df = 1, 529$; $P < 0.0001$; region \times treatment, $F = 12.54$, $df = 1, 528$; $P = 0.0004$).

At European sites the reproductive structures on *C. stoebe* (flower buds and heads, and seedheads combined) increased 52–520% with removal of neighbors (Fig. 1B). At Montana sites, removing neighbors changed the

production of reproductive structures from a decrease of 21% to a maximum increase of 62%; a 7.5-fold difference in responses between regions (region, $F = 29.14$; $df = 1, 539$; $P < 0.0001$; region \times treatment, $F = 5.05$, $df = 1, 568$; $P = 0.025$). In Montana, the effect of removing neighbors was not significant at any site for reproductive structures; whereas in Europe the effect of removing neighbors was significant at four of the five sites.

The only European site where we did not find a significant effect of removing neighbors was Barcs, where more than half of the target plants had already begun to bolt at the beginning of the experiment. However, we found no relationship between the mean initial plant size at a site (length of longest leaf) and the mean response to neighbor removal in Europe (regression, size vs. response, $P = 0.731$) or North America ($P = 0.981$).

DISCUSSION

Despite the common perspective that competition plays a role in the success of invasive species in their nonnative ranges, to our knowledge no study prior to this one has experimentally compared differences in competitive intensity for an invasive plant species in its native range and nonnative range. We found 6.5- to 7.5-fold higher responses of target *C. stoebe* to removal of neighbors in its native range than in its nonnative range. In other words, in the nonnative range of *C. stoebe* other plant species provided very weak competitive resistance. We can think of four possible non-mutually exclusive reasons for this biogeographical difference. First, stronger competitive effects in Europe were due to greater productivity and biomass of the native community. Second, species in intermountain grasslands are weak competitors relative to others in the greater global species pool. Third, *C. stoebe* possesses traits that yield more powerful competitive abilities in its nonnative range than in its native range. Fourth, North American *C. stoebe* genotypes might be competitively stronger than European genotypes (due to genetic drift and/or post-introduction selection), but this genetic difference might be manifest through one of the other mechanisms.

Growth rates and biomass of interacting species can have powerful effects on short-term competitive outcomes. *Centaurea stoebe* occupies a different climatic niche in its nonnative range of Montana, with lower total precipitation and much lower growing season precipitation than in their native range (Treier et al. 2009). We did not measure productivity, but the grassland sites in Europe are more productive than the sites in Montana, due to the two- to three-fold differences in precipitation between regions, a pattern consistent with general climatic differences between the native and nonnative ranges of *C. stoebe* (Broennimann et al. 2007). The mean annual productivity of intermountain and mixed-grass prairie in the region of our experiments ranges from 160 g/m^2 (J. L. Maron, unpublished data) to 188 g/m^2 (Vermeire et al. 2009); whereas productivity in the native range of *C. stoebe* can



PLATE 1. (Left) A native *Gaillardia aristata* surviving in a sea of the invasive *Centaurea stoebe*. (Right) Palouse prairie in western Montana (USA), with the lead author looking for knapweed plants for the experiment. Photo credits: (left) R. Callaway; (right) Dan Atwater.

be much higher. For example, in Hungarian loess grasslands, peak productivity ranges from ~ 395 to 535 g/m^2 (Molnár 2006, Nagy and Tuba 2008). However, productivity in German grasslands where *C. stoebe* occurs is lower, varying from 60 to 310 g/m^2 (K. Süß, *personal communication*; derived from Süß et al. 2007). In 2010 we visually estimated total vegetation cover in 20 randomly located 40 cm diameter rings, and measured maximum vegetation height, at each of two sites in Europe and each of five sites in Montana. For the sites combined in each region, mean vegetation cover at the European sites was $74.4\% \pm 3.1\%$ vs. $62.5\% \pm 2.4\%$ in Montana. Mean vegetation height at the European sites was $62.8 \pm 3.6 \text{ cm}$ vs. $41.2 \pm 2.0 \text{ cm}$ in Montana. As another metric of potential differences in productivity between regions, the final biomass of *C. stoebe* without competitors was $3.51 \pm 0.43 \text{ g}$ in Europe, compared to $1.49 \pm 0.09 \text{ g}$ in Montana. Thus, this also suggests roughly a twofold difference in productivity in the native range, but this estimate is confounded by the larger size of *C. stoebe* plants at the beginning of the experiment in the native range (young plants were much harder to find); initial leaf length was $16.02 \pm 0.77 \text{ cm}$ in Europe vs. $6.54 \pm 0.16 \text{ cm}$ in Montana. For the six sites at which we measured height, we regressed the proportional competitive effect at a site against mean vegetation height and found that mean height was significantly correlated with competitive intensity ($P = 0.0347$). While it is highly likely that changes in the climatic niche and greater biomass and productivity at the European sites contributed to the stronger competitive suppression of *C. stoebe*, to explain the 6.5- to 7.5-fold differences in competitive effects European vegetation would have had to have higher per mass effects than North American vegetation. While this is certainly

possible for a number of reasons, in the only relevant experimental test we know of in the literature, the competitive “intensity,” which was our metric of competition as well, of matrix vegetation on *Poa pratensis* did not vary significantly over a greater than six-fold difference in community biomass (Brooker et al. 2005). However, competitive “importance” decreased with decreasing biomass.

Evidence suggesting that *C. stoebe* competes in inherently different ways with European vs. North American species is mixed. In one of two experiments with *C. stoebe* from many different populations, He et al. (2009) found that *C. stoebe* was a much better competitor against a suite of North America plants than against congeners native to Romania. These results corresponded well with differences in the effects of experimentally applied (\pm)-catechin, a chemical in the root exudates of *C. stoebe* (Tharayil and Treibwasser 2009). However, whether *C. stoebe* produces enough (\pm)-catechin to be allelopathic, and thus to be a key novel competitive trait, is uncertain (Vivanco et al. 2010). Also, in a second experiment using just one population from North America and Europe, and in which North American and European native species were collected from a broader range of sites, He et al. (2009) found that the competitive effects of *C. stoebe* were slightly stronger against European species than against North American species, the opposite of the previous experiment. Recently, Aschehoug et al. (2012) found that *C. stoebe* was a much better competitor against a suite of North American grass species than native grasses from Europe, and also that these competitive effects against North American species were enhanced by fungal endophytes. Fungal endophytes did

not increase the competitive effect of *C. stoebe* on native European grasses.

Furthermore, post-introduction selection may contribute to increased competitiveness in *C. stoebe* as compared to native European populations as tetraploid plants from North America achieve greater growth rates than both tetraploids and diploids from the native range (Henery et al. 2010; also see Ridenour et al. 2008). Greater accumulation of biomass in rapidly growing young North American tetraploids may represent evidence for a trade-off between growth and defense because it compliments previous findings on lower defense-related gene expression in North American tetraploids (Broz et al. 2009).

The limited effects of competition on *C. stoebe* performance that we found in Montana have been partially corroborated by similar results from Colorado. Knochel and Seastedt (2010) found that neighbor removal had no effects on *C. stoebe* size or flower production at one grassland site in Colorado, although performance was enhanced by neighbor removal at a second site. Although these results, like ours, suggest that *C. stoebe* does not encounter high competitive suppression where it has been introduced, we know from greenhouse and common garden competition experiments that North American natives are capable of exerting strong competitive pressure on *C. stoebe* (Ridenour and Callaway 2001, Callaway et al. 2004, He et al. 2009). As well, assembled diverse communities of natives can resist knapweed invasion (and impact) to a greater extent than more species poor communities (Pokorny et al. 2005, Maron and Marler 2007, 2008b). Furthermore, our protocol used young plants that had already established, and thus, we cannot know about the effect of competition on recruitment and establishment of *C. stoebe* propagules. Thus, our results should not be interpreted as a demonstration that *C. stoebe* does not suffer at all from competitive effects imposed by North American natives. Rather, our major conclusion is simply that the level of this neighborhood competition appears to be much weaker in intermountain grasslands than it does in native European sites.

Because of the scarcity of sites in Europe where *C. stoebe* reaches densities like those in Montana, we selected sites in Europe where *C. stoebe* was quite abundant relative to other potential sites; whereas in Montana we selected sites where *C. stoebe* was relatively sparse so that its competitors would be native species and not conspecifics. Thus, we may have chosen sites in Europe where *C. stoebe* experiences its most local advantages, and sites in Montana that do not represent sites where *C. stoebe* performance is the greatest relative to natives; i.e., the sites where *C. stoebe* forms near-monocultures. If so, our results are very conservative. However, we also caution that the results of removal experiments in the field have the potential to be confounded by either "apparent competition" or apparent facilitation indirect effects (Callaway et al. 1996). In

other words, removal of heterospecific neighbors in the native range, where generalist herbivore (Schaffner et al. 2011) attack may be greater, may make target *C. stoebe* easier to locate and attack. If this indirect effect is stronger in the native range than in the nonnative range, we would be overestimating competitive effects.

Our results show strong biogeographical differences in competitive effects of native vegetation on *C. stoebe* and indicate that invasions are not simply the product of disturbance affecting either natives or exotics. We do not know the mechanism for this difference, but these results are the first of their kind and suggest that general competitive interactions contribute to the striking dominance of *C. stoebe* in some parts of North America. In a broader context, our results suggest that escape from strong interspecific competition in the native range may contribute substantially to invasive success. What are needed now are longer term experiments, potentially including reciprocal transplants between ranges, that examine how competition influences multiple life stages of invasive species and how this ultimately affects the relative abundance and impacts both in invaded and native ranges.

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APPENDIX

Sites at which neighbor-removal competition experiments were conducted with *Centaurea stoebe* as the target (*Ecological Archives* E092-191-A1).